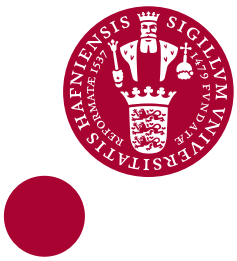

Multi-taxon inventory reveals highly consistent biodiversity responses to ecospace variation

Brunbjerg, Ane Kirstine; Bruun, Hans Henrik; Dalby, Lars; Classen, Aimée T.; Fløjgaard, Camilla; Frøslev, Tobias G.; Hansen, Oskar Liset Pryds; Høye, Toke Thomas; Moeslund, Jesper Erenskjold; Svenning, Jens-Christian; Ejrnæs, Rasmus

Published in:
Oikos

DOI:
10.1111/oik.07145

Publication date:
2020

Document version
Publisher's PDF, also known as Version of record

OIKOS

Research

Multi-taxon inventory reveals highly consistent biodiversity responses to ecospace variation

Ane Kirstine Brunbjerg, Hans Henrik Bruun, Lars Dalby, Aimée T. Classen, Camilla Fløjgaard, Tobias G. Frøslev, Oskar Liset Pryds Hansen, Toke Thomas Høye, Jesper Erenskjold Moeslund, Jens-Christian Svenning and Rasmus Ejrnæs

A. K. Brunbjerg (https://orcid.org/0000-0003-0666-6535) ✉ (akb@bios.au.dk), L. Dalby, C. Fløjgaard, T. T. Høye (https://orcid.org/0000-0001-5387-3284), J. Erenskjold Moeslund and R. Ejrnæs, Dept of Bioscience, Aarhus Univ., DK-8410 Rønde, Denmark. – H. H. Bruun, Dept of Biology, Univ. of Copenhagen, Copenhagen, Denmark. TTH also at: Arctic Research Centre, Aarhus Univ., Aarhus, Denmark. – A. T. Classen,Rubenstein School of Environment and Natural Resources, The Univ. of Vermont, Burlington, VT, USA, and: The Gund Institute for Environment, Univ. of Vermont, Burlington, VT, USA. – T. G. Frøslev, GLOBE Institute, Univ. of Copenhagen, Copenhagen, Denmark. – O. L. Pryds Hansen and J.-C. Svenning (https://orcid.org/0000-0002-3415-0862), Section for Ecoinformatics and Biodiversity, Dept of Bioscience, Aarhus Univ., Aarhus, Denmark, and: Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Dept of Bioscience, Aarhus, Denmark.

Oikos
129: 1381–1392, 2020
doi: 10.1111/oik.07145

Subject Editor: Paul Caplat
Editor-in-Chief: Dries Bonte
Accepted 19 May 2020

Amidst the global biodiversity crisis, identifying general principles for variation of biodiversity remains a key challenge. Scientific consensus is limited to a few macroecological rules, such as species richness increasing with area, which provide limited guidance for conservation. In fact, few agreed ecological principles apply at the scale of sites or reserve management, partly because most community-level studies are restricted to single habitat types and species groups. We used the recently proposed ecospace framework and a comprehensive data set for aggregating environmental variation to predict multi-taxon diversity. We studied richness of plants, fungi and arthropods in 130 sites representing the major terrestrial habitat types in Denmark. We found the abiotic environment (ecospace position) to be pivotal for the richness of primary producers (vascular plants, mosses and lichens) and, more surprisingly, little support for ecospace continuity as a driver. A peak in richness at intermediate productivity adds new empirical evidence to a long-standing debate over biodiversity responses to productivity. Finally, we discovered a dominant and positive response of fungi and insect richness to organic matter accumulation and diversification (ecospace expansion). Two simple models of producer and consumer richness accounted for 77% of the variation in multi-taxon species richness suggesting a significant potential for generalization beyond individual species responses. Our study widens the traditional conservation focus on vegetation and vertebrate populations unravelling the importance of diversification of carbon resources for diverse heterotrophs, such as fungi and insects.

Keywords: abiotic environment, carbon resources, environmental DNA, heterotrophs, primary producers, taxonomic aggregation

NORDIC SOCIETY OIKOS

www.oikosjournal.org

Introduction

For centuries, ecologists have struggled to understand and explain spatial and temporal variation in biodiversity, with increasing societal attention motivated by the global biodiversity crisis (Díaz et al. 2019). While land-use change is identified at a global scale as the most important present and future driver of biodiversity loss in terrestrial and freshwater systems (Titeux et al. 2016, Díaz et al. 2019), there is less agreement about the underlying causes for variation in biodiversity. Most models and theories of biodiversity refer to specific taxonomic groups and ecosystems (Fagerström and Westoby 1997, Lawton 1999, Blaxter et al. 2005, Brunbjerg et al. 2018, Jepson et al. 2018, Moeslund et al. 2019), leaving us with no general rules and ecological theories of variation in local diversity and without prioritization tools at the local spatial scales where practical conservation planning and management takes place. Several studies have investigated the potential for using selected species groups to represent the wider conservation interests, but based on a global meta-analysis Westgate et al. (2014) concluded that the data undermines the assumption that a taxonomic subset can represent the wider biodiversity. The disappointing conclusion has been somewhat contradicted or modified lately by studies showing promising potential for cross-taxon congruence in species composition and compositional turnover (β-diversity) (Prober et al. 2015) and also for species richness, but only after accounting for environmental variation (Duan et al. 2016, Brunbjerg et al. 2018). In addition, measures of 'genetic diversity' and turnover (e.g. number of operational taxonomic units – OTUs (Blaxter et al. 2005)) may soon become a genuine alternative to classical observed diversity measures (Frøslev et al. 2019). Along this line of reasoning, we set out to test the hypothesis that terrestrial multi-taxon diversity can be predicted across contrasting environments without detailed consideration of an intractable diversity of taxonomic groups, response groups or habitat types. We are thus not investigating the surrogacy hypothesis per se, but rather the idea that multi-taxon diversity can be predicted from a low-dimensional ecological space, ignoring the possible multitude of response shapes of the individual taxonomic groups, OTUs or species.

We applied the recently proposed ecospace framework (Brunbjerg et al. 2017, 2018, 2019, Jepson et al. 2018, Moeslund et al. 2019) for a formal and structured quantification of environmental variation. Ecospace represents the total environment in space and time, in which the individual (species) colonizes, grows, reproduces and dies or goes extinct. Ecospace may help reduce environmental complexity to a tractable number of dimensions and measurable variables. We have proposed to subdivide ecospace into three components each signifying important aspects of an area for its potential biota: 1) The abiotic environment (ecospace position), 2) The accumulation and diversification of organic matter (ecospace expansion) and 3) The spatio–temporal continuity (Brunbjerg et al. 2017).

The position of a site in n-dimensional environmental hyperspace (e.g. mean values of soil moisture, pH, soil fertility and temperature) is essential to sessile organisms like plants and soil–fungi unable to move across their local environment (Fagerström and Westoby 1997), but even mobile animals respond to abiotic conditions when they select their habitat (Dufrêne and Legendre 1997). Expansion, i.e. the accumulation and diversification of organic matter, is particularly important as an energy source for consumers (Elton 1966), but may also provide substrate for e.g. epiphytic plants and lichens (Ellis 2012). Expansion presupposes primary production and subsequent differentiation into leaves, roots, stems, flowers, bark, wood, dung etc. On evolutionary time scales, every differentiated pool of live or dead organic matter has provided opportunity for heterotrophic niche differentiation and speciation (Futuyma and Agrawal 2009).

The spatial continuity of habitats is expected to be particularly important for short-lived and poorly-dispersed species moving among patches varying in suitability over time, but less important for species with long distance dispersal (Thomas Chris 2000). Temporal continuity on the other hand should be particularly important for organisms with limited dispersal ability and high persistence, such as some plants and fungi, which are sensitive to changing habitat conditions (Fagerström and Westoby 1997).

The aim of this study was to investigate the hypothesis that multi-taxon α-diversity, including 'genetic richness' (Blaxter et al. 2005) from environmental DNA, can be treated as a general, predictable biotic response to environmental variation represented by a low number of key factors. We assess this using ecospace as a framework for guiding the study design, environmental mapping and data analysis.

Methods

During 2014–2017, we collected data from 130 sites (40 × 40 m) within 15 clusters nested in five regions across Denmark (Fig. 1). We allocated 100 sites to span the most important natural gradients affecting biodiversity in Denmark i.e. gradients in soil fertility, soil moisture and successional stage: from nutrient rich to nutrient poor, from dry over moist to wet and from open, closed and forested vegetation. 90 of these sites were selected randomly within 18 predefined strata, whereas 10 sites were selected by the amateur natural historian community to represent biodiversity hotspots for different species groups. The remaining 30 sites were sampled randomly from six strata cultivated for production: plantations (beech, oak or spruce) and fields (rotational, grass leys or set aside). Randomization was achieved by selection of sampling areas and potential sites from a large nationwide dataset of vegetation plots in semi-natural habitats distributed across the entire country (n = 96 400 plots of 78.5 m^2 each, <https://naturdata.miljoeportal.dk/>) – for some rare strata we also consulted local experts. To minimize spatial autocorrelation, the minimum distance among

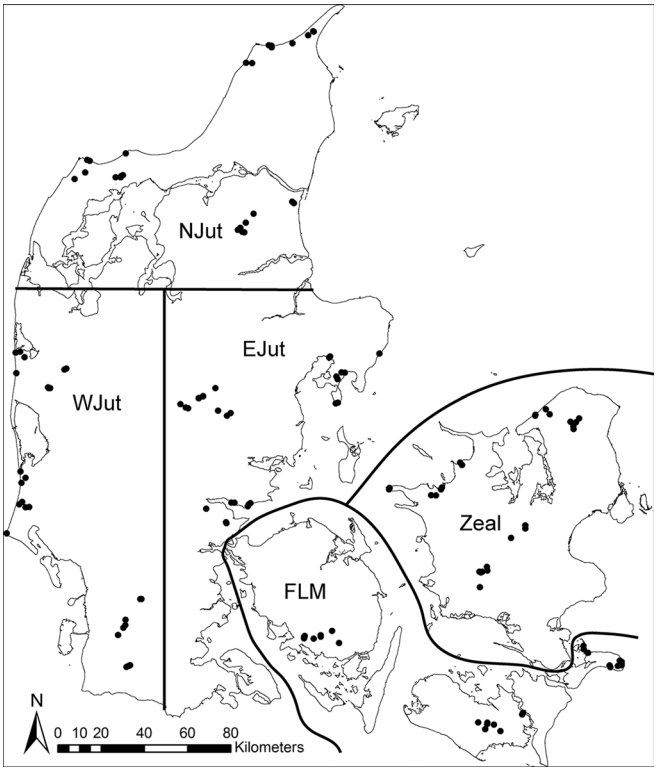

Figure 1. Map of Denmark showing the location of the 130 sites grouped into 15 clusters within five regions (NJut: Northern Jutland; WJut: Western Jutland; EJut: Eastern Jutland; FLM: Funen, Lolland, Møn; Zeal: Zealand).

sites was 500 m with a mean nearest distance among sites of 2291 m. Within each site, we sampled vascular plants, mosses lichens, fungi and arthropods, and we included metabarcoding of DNA from soil samples and insect traps to reflect the 'genetic richness' (i.e. number of operational taxonomic units – OTUs (Blaxter et al. 2005)) of all eukaryotes, fungi and arthropods, the group names referring to the targets of three different primers. Furthermore, we collected data reflecting ecospace i.e. abiotic position, biotic expansion and spatio-temporal continuity. For further details on site selection and data collection, see Brunbjerg et al. (2019). All field work and sampling was conducted in accordance with Responsible Research at Aarhus University and Danish law.

Ecospace position variables

Ecospace position represents the abiotic factors affecting species occurrence directly via environmental filtering (Brunbjerg et al. 2017) or indirectly causing variation in species pools developed over evolutionary and historical temporal scales. The following variables represented abiotic position:

Ecological species pool index

We developed the ecological species pool index to reflect the importance of evolutionary and historical contingency on local community assembly. The species pool was only developed for vascular plants as we did not have access to independent data for other species groups (but see host plant indices for fungi and insects below). We extracted Ellenberg indicator values (Ellenberg et al. 1991) for all vascular plants considered part of the Danish flora (<www.allearter.dk>). Ellenberg indicator values specifies plant optima for ecological conditions and we used light (Ellenberg L), moisture (Ellenberg F) and pH (Ellenberg R) as predictors of species pool size. We avoided Ellenberg nutrient preference, as this indicator implies competitive hierarchies. We used a quasi-poisson GAM-model (k = 3) with Ellenberg values as explanatory variables and the number of plant species associated with each unique combination of Ellenberg F, L and R as a response variable (the three variables were normalized to 0–1 before modelling). To estimate the species pool index for each of the 130 sites we predicted the number of plants based on the GAM-model and the unweighted site mean of Ellenberg F, L and R values. The species pool index was log-transformed as this provided the best linear fit to observed species richness.

In order to avoid statistical modelling involving several correlating indicators for the same latent variable, we calculated indices for soil fertility and soil moisture by integrating a range of abiotic measures indicating these soil properties.

Soil fertility index (SFI)

Soil fertility is a complex attribute involving cycling, holding capacity, release rate, immobilization, leaching etc. and nutrient availability changes over the season. For each site; we calculated SFI as the predicted value from the best linear model (of all sites) of site mean Ellenberg N (Ellenberg et al. 1991) (plant-based bioindication of nutrient status) as a function of soil calcium (Ca), leaf nitrogen (N), leaf N:phosphorus (NP) and soil type (Supplementary material Appendix 1 Table A1).

Soil moisture index (SMI)

Soil moisture is a complex attribute reflecting local hydrology as well as precipitation and soil moisture varies between seasons and years. We calculated a soil moisture index for each site using the predicted values from the best linear model (of all sites) of mean Ellenberg F (Ellenberg et al. 1991) (plant-based bioindication of soil moisture) as a function of mean precipitation in 2001–2010 (10 × 10 km grid resolution) and measured site soil moisture (trimmed mean of 16 measures per site taken with a FieldScout TDR 300 Soil Moisture Meter in May 2016).

Soil pH

We measured soil pH on soil bulk samples (mix of four samples per site: depth = 0–10 cm, 5 cm diameter).

Light

We measured light intensity (lux) reflected microclimate in each site using data loggers.

Air temperature

Air temperature (°C) reflected microclimate in the sites and was measured using data loggers.

Boulders

We measured the presence of boulders (diameter > 20 cm) within each site using presence–absence because there is a low density of boulders on the Danish landscape. While boulders are 'habitats' for epilithic mosses and lichens, here we defined them as position because of their abiotic nature.

Ecospace expansion variables

Expansion is comprised of organic matter that species can live on (surfaces) or from (resources). Expansion variables reflect both quantitative (amount of organic matter) and qualitative (diversity of organic matter) aspects.

Pools of organic matter

1) Dung of herbivores (presence/absence of dung of hare, deer, sheep, cow or horse).
2) Litter mass ($g\,m^{-2}$ of four litter samples within a 21 × 21 cm frame per site).
3) Flowers. The density of flowers of insect-pollinated plants presenting flowers within the site (sum of estimates from June to August 2014 and April 2015). Flower density was recorded using plotless sampling (BDAV3 sensu White et al. 2008 as described in Brunbjerg et al. 2019) and weighted by flower surface area as follows: if flower surface area < 4 cm^2 flower density was multiplied by 2, if flower surface area 4–10 cm^2 flower density was multiplied by 7 and if flower surface area > 10 cm^2 flower density was multiplied by 15. The multiplication factors represent the median number for each flower volume class with the underlying assumption that nectar and pollen volume relate to flower volume.
4) Dead wood: diameter and length of coarse woody debris (> 20 cm diameter, min length 1 m) was recorded and volume/ha was calculated.
5) Fine woody debris: density of fine woody debris (5–20 cm diameter and > 1 m, or >20 cm and < 1 m), including tree stumps within the site was recorded by plotless sampling (White et al. 2008).
6) Density of large trees: the number of large live trees (> 40 cm DBH) within the site was recorded.
7) Organic matter: percentage of the 0–10 cm soil core that was categorized as organic soil (average of four soil samples taken in each site).
8) Soil organic C content: % soil C in 0–10 cm soil layer ($g\,m^{-2}$ average of four soil samples taken in each site).
9) The number of plant species per site: as plants make up a carbon pool and structural habitats for fungi and arthropods (Castagneyrol and Jactel 2012) standardized number (subtracting the mean and dividing by the SD) of plant species per site was used as expansion variable in fungi and arthropod models as well as eDNA eukaryote, eDNA fungi and flying insects models. Although plant richness is a major predictor of consumer richness, it must be excluded from the total richness model in order to avoid circularity.

Shrub and tree layer

We subtracted the digital elevation model (DEM (Danish Ministry of Environment 2015)) (40 × 40 cm resolution) from the digital surface model (40 × 40 cm resolution) to create a grid representing the above-ground vegetation height. From this, we calculated two variables for each site: The 90th percentile for returns > 3 m within the site reflecting the height of mainly trees (called tree layer) and the 90th percentile for returns 30 cm–3 m reflecting the height of the shrub layer. The shrub layer was recalculated to a presence/absence variable splitting the data at 2 m, motivated by a pronounced bimodal distribution of data points.

Indices for abundance of insect host plants and fungi host plants

In order to produce indices reflecting the availability of possible host plants for insects and fungi, we retrieved information on the associations between vascular plants and their consumers (fungi and insects). For fungi, we used observational data from the Danish Fungal Database (<https://svampe.databasen.org>) and for insects, we used accounts from an insect host plant database for north-west Europe hosted at the Biological Records Centre (<www.brc.ac.uk/dbif/hosts.aspx>). Some consumers have links to many plant species while others are specialized to a single species or genus of plants. We assured equal importance of each consumer-link by weighting each link inversely with the number of plant genera involved with the consumer in question. Links reported to the genus level were attributed to all plant species within that genus. After summing all observed links for each plant species, we produced models predicting plant host attractiveness using plant functional traits as explanatory variables (Bruun et al. 2020). The model for fungi used ectomycorrhizal capacity, regional nativeness, plant size, life form and distributional range and explained 66% of the observed link score and the model for insects used ectomycorrhizal capacity, phylum, plant size, life form and distributional range and explained 46% of observed link score. We used the models to predict a value for each plant species in our data set, and we used the sum of values for the species of a site weighted by species abundance score in the site (from 1 to 3) as index for host plant availability for fungi and arthropods respectively.

Ecospace continuity variables

Continuity is the extent of the site habitat (position and expansion) in time and space.

Geographical species pool

The geographical species pool reflects the impact of historical processes on the species pool size under the assumption that immigration is ongoing and geographically directed (from southeast towards northwest) and that the Danish flora is not yet saturated. We estimated a geographical species pool for each site from predictions of a GAM model on vascular plant species richness as a function of geographic coordinates using an independent data set from a national Atlas Survey of

vascular plant species in 1300 reference quadrats of 5 × 5 km (Hartvig 2015).

Spatial continuity

We estimated spatial continuity by assessing the amount (%) of natural areas within four different distances from the focal site (500, 1000, 2000 and 5000 m). Spatial continuity of the habitat type of the site was estimated by visual interpretation of aerial photographs and additional information from land mapping of woodlands, fields, grassland, heathland, meadows, salt marshes and mires. The four buffer sizes were similar and highly correlated. The 500 m buffer was used for analyses as most of the studied species were expected to have relatively limited dispersal and small area requirements.

Temporal continuity

Temporal continuity was estimated by time since major land use change within the 40 × 40 m site. For each site, a temporal sequence of aerial photos and historical maps was inspected starting with the most recent photos (photos from 2014, 2012, 2010, 2008, 2006, 2004, 2002, 1999, 1995, 1968, 1954, 1945) and ending with historical maps reflecting land use in the period 1842–1945. Temporal continuity (the year in which a change could be identified) was reclassified into a numeric 4-level variable: 1: 1–14 years, 2: 15–44 years, 3: 45–135 years, 4: > 135 years.

Co-variables

We include the following co-variables to account for a possible spillover of species by passive colonization from natural habitats in the surrounding landscape as well as a possible effect of within-site heterogeneity, increasing opportunities for niche differentiation. Co-variables were log transformed if transforming improved the distribution (visual inspection).

Natural landscape

We calculated the % share of natural or extensively used areas (forests, wetlands, heathlands and grassland) in 1 × 1 km quadrats across Denmark and interpolated these using Spline in Arcgis 10.2.2, Weight 0.5, number of points 9 (Ejrnæs et al. 2014). Site values were then extracted from the interpolated map based on geographical coordinates.

Heterogeneity variables

Site heterogeneity was calculated for soil moisture, soil fertility, soil pH and tree and shrub layer height as the variance of the variables measured within sites described above.

Soil moisture variability

The variance of trimmed mean of 16 evenly distributed measurements of soil moisture within each site taken with a soil moisture meter in May 2016.

Soil fertility variability

The variance of four soil fertility index values per site (soil fertility index = predicted values of a linear model of Ellenberg N as a function of leaf N, leaf NP, soil P, soil Ca and soil class). Soil fertility variability was log transformed due to skewness.

Soil pH variability

The variance of four evenly distributed soil pH measurements per site.

Tree layer variability

The variance of the 90th percentile for returns > 3 m within the site reflecting the variability of the height of mainly trees (see description of the tree layer expansion variable above).

Shrub layer variability

The variance of the 90th percentile for returns 30 cm–3 m reflecting the variability of the height of the shrub layer (see description of the shrub layer expansion variable above).

All explanatory variables were standardized except for presence/absence variables (boulders, dung of herbivores and shrub and tree layer). For distributions of explanatory variables see Supplementary material Appendix 1 Fig. A1.

Response variables

We divided species into response groups according to taxonomy (plants, mosses), trophic level (macrofungi) and trophic level and mobility (invertebrates). Grouping is complicated for insects because the biology and mobility may depend on live stage. Hoverflies for example have larval stages spanning from detritivores over predators to galling herbivores, whereas the adult flies mainly feed on flowers. An entirely trophic categorization is further intractable given that many resource strategies in insect larvae are unknown. Moreover, the species richness response may rely on the mobility and preferences of the observed imago rather than the occupation of the larvae. We therefore decided to follow a pragmatic division based on biological reasoning.

The response groups of our study included vascular plants, mosses, lichens, decomposing fungi, symbiotic fungi, flying insects (highly mobile insects dependent on ephemeral food sources such as dung, flowers, fungi and dead wood), herbivores (mobile insects dependent on live, sessile plants), detritivores (invertebrates dependent on dead carbon sources) and predators (arthropods dependent on live animals). Distribution of species richness and details on grouping can be seen in Supplementary material Appendix 1 Fig. A2, Table A2, respectively. In order to investigate the potential for generalization across species groups we pooled species into the larger groups of producers (vascular plants, mosses and lichens), consumers (fungi and arthropods) and total (producers and consumers). In addition, we used richness of OTUs (operational taxonomic units (Blaxter et al. 2005)) of eukaryotes and fungi from soil eDNA and arthropods from eDNA extracted from ethanol from Malaise traps. For details on collecting species and eDNA data see Brunbjerg et al. (2019).

eDNA datasets

The preparation of the fungal (ITS2) and eukaryote (18S) eDNA datasets have been published in Fløjgaard et al. (2019)

and Frøslev et al. (2019) respectively. The arthropod DNA dataset was produced by extracting DNA from the ethanol from the bulk insect Malaise traps and metabarcoding with the arthropod specific COI primers ZBJ-ArtF1c and ZBJ-ArtR2c (Zeale et al. 2011). 45 ml ethanol and 1.5 ml of 3 M sodium acetate were added to a 50 ml centrifuge tube, and left in a freezer for DNA precipitation overnight, then centrifuged for 40 min. The dried pellet was extracted with the Qiagen DNeasy blood and tissue kit with minor modifications. The extracted DNA was normalized, amplified, sequenced and analyzed according to the overall procedures described in Brunbjerg et al. (2019). As for the eukaryote and fungal datasets OTU tables were constructed following the overall pipeline suggested in Frøslev et al. (2017), to derive OTUs that approximates species level delimitation. This consisted of an initial processing with DADA2 (ver. 1.8) (Callahan et al. 2016) to identify exact amplicon sequence variants (ESVs, see Callahan et al. 2017) including removal of chimeras and post-clustering curation using LULU (Frøslev et al. 2017). Taxonomic assignment was done with a custom script (as in Fløjgaard et al. 2019). OTUs not assigned to Arthropoda were discarded before further analyses. Data from the two different collecting events were handled separately and the sequences were then combined for each site. Sequencing data for arthropods and links to files and scripts necessary to replicate analyses are deposited at GitHub at <https://github.com/tobiasgf/biowide_synthesis>.

Explanatory variables and statistical analyses

We built generalized linear models (GLMs) to predict species richness of selected response groups based on the best selection of ecospace variables. In addition, we built GLMs to predict the summed richness of vascular plants, mosses and lichens (producers) and fungi and invertebrates (consumers). Finally, we built an overall species richness model predicting the total richness of all observed species (summed richness of vascular plants, mosses, lichens, fungi and invertebrates).

For each model, we made a preliminary screening and selection of relevant variables, only keeping variables with a hypothesized relationship to the species group in question. We further constrained the response direction and shape to ecologically plausible responses (Burnham and Anderson 2002, Zuur et al. 2010) implying an exclusion of negative effects of expansion, continuity and heterogeneity variables on species richness – based on the reasoning that more resources, more diverse resources, more environmental variation and increasing temporal and spatial continuity are all hypothesized to have one-sided positive effects on richness. We select variables and constrain responses to reduce the risk of including spurious correlations in the models and thereby covering important causal relationships (Supplementary material Appendix 1 Table A3).

Log transformation was preferred if model improvement was indicated by Akaike's information criterion (AIC) (Johnson and Omland 2004). The number of explanatory variables were further reduced in order to avoid collinearity (VIF values < 3, Zuur et al. 2010). A preliminary set of full models was built using all remaining variables: a general linear mixed poisson model (GLMM) with region as random variable and a GLM with poisson errors using the log link function. We selected the best model type using the $\Delta AIC < 2$ criterion (Burnham and Anderson 2002). Negative binomial errors were used if overdispersion was detected (Hilbe 2011) in poisson models. We included a quadratic term of the abiotic position variables if the full model significantly improved according to the $\Delta AIC < 2$ criterion. Expansion and continuity variables having a negative effect in the full model after variable transformation and adding of quadratic terms were deleted sequentially starting with the variable with the lowest z-value. The residuals of full models were checked for model misfit, overdispersion and spatial autocorrelation using simulated residuals and R package DHARMa (Hartig 2016). We used backwards elimination of explanatory variables using the $\Delta AIC < 2$ rule to reduce full models to final models. For the flying insect and DNA flying insect models, significant autocorrelation was detected in the GLM negative binomial model ($p = 0.004$ and $p = 0.006$ in a Moran's I test, respectively). To avoid effects of autocorrelation on model selection, we used non-parametric model selection (five-fold cross validation) for these models while applying the $\Delta AIC < 2$ rule.

Model performance of the final models were evaluated using five-fold cross-validation. To evaluate the effect of generalizing we compared the performance of models on aggregated species groups with the performance of the corresponding models on the individual species groups. In order to do this, Pearson product correlations between the sum of predictions from specific group models and the sum of observed species of producers, consumers and total (referred to as the summed predictions from nine species group models and summed predictions for producers and consumers), were calculated, respectively.

Variation partitioning was calculated on final models for each component of ecospace (position, expansion, continuity and co-variables) as follows:

$$\text{adjusted deviance explained}\left(\text{best model}\right) - \text{adjusted deviance explained}\left(\text{model without target ecospace component}\right)$$

Data exploration was applied following Zuur et al. (2010). All analyses were performed in R ver. 3.5.0 (<www.r-project.org>).

Results

Individually, the nine species richness models explained between 17% (predatory arthropods) and 62% (decomposing fungi) of the variance in species richness across environmental gradients (Fig. 2). When we pooled species into producers and consumers, the explained variation based on

cross-validated predictions was comparable to the individual models (producers: 46%, predictions producers: 53%; consumers: 71%, predictions consumers: 68%). The model for species richness of all groups explained 51% of the variation in biodiversity across sites, considerably less than the predictions from the sum of all nine separate species group models (74%). However, the summed predictions from the models of producers and consumers explained 77% of total species richness. Based on this result, we focused further reporting of results on models of producer and consumer biodiversity (Fig. 3). Producer richness was primarily explained by position (Fig. 3a); increasing with soil pH, intermediate nutrient status, extreme soil moisture (wet/dry sites), presence of boulders and with the ecological plant species pool size. The ecological species pool index (index based on vascular plants that reflect the importance of evolutionary and historical contingency on local community assembly) reveals that there are more vascular plants in the Danish flora which prefer relatively high incoming light, intermediate soil moisture and relatively high soil pH (Supplementary material Appendix 1 Fig. A3). Presence of a shrub layer also promoted producer richness. Finally, producer richness increased with temporal continuity. Variance partitioning revealed that position explained most variation in producer richness with minor

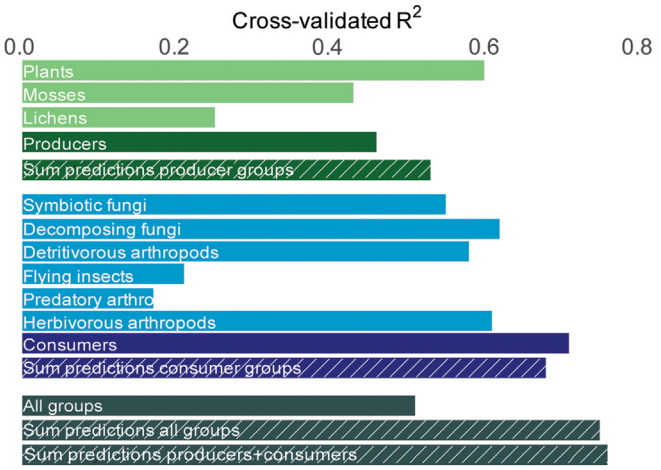

Figure 2. Cross-validated R^2-values (%) for the best GLM negative binomial models explaining species richness in 130 sites from environmental and geographic variables. Green – producers, blue – consumers, dark grey – all groups species richness. Hatched bars represent explained variation from pooling the predictions of individual models and they are included for evaluating the effect of taxonomic aggregation to the level of producers, consumers and all groups species richness. For example, the hatched dark green bar is the correlation between the pooled predictions from the plant, moss and lichen models respectively and the observed richness for all of these groups. This compares to the solid dark green bar representing the correlation between the predictions from a model including all producer groups and the observed values. For all groups, the first hatched bar represents the correlation for the summed predictions from all nine species group models, whereas the second hatched bar represents the correlation for the summed predictions for the producer and the consumer models.

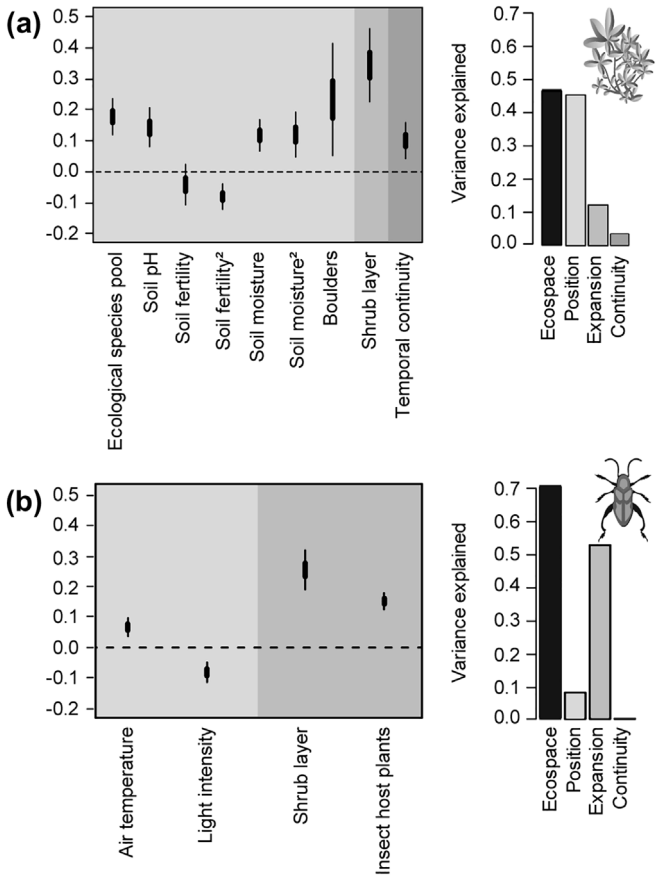

Figure 3. Coefficient plot of the best models for (a) producer (plants, mosses, lichens) and (b) consumer (fungi, arthropods) richness in the 130 sites (left-hand panel) and explained variance for ecospace and its components (position, expansion, continuity; in the right-hand panel). Explanatory variables are standardized and shaded according to ecospace components: position – light grey, expansion – grey, continuity – dark grey. Thick (inner) bars represent ± 1 standard error, thin (outer) bars represent ± 2 SE.

contributions from expansion and continuity (Fig. 3a). Consumer richness increased with presence of a shrub layer, and a high index of insect host plant abundance (Fig. 3b). For position, consumer richness increased with air temperature and decreased with incoming light. We found no effect of continuity on consumer richness. Variance partitioning revealed that most variation in consumer richness could be explained by expansion compared to a minor contribution from position (Fig. 3b).

The following expansion variables promoted species richness for the individual response groups: litter mass for decomposing fungi, soil carbon content for arthropod detritivores and flying insects, dung for decomposing and symbiotic fungi as well as total species richness, dead wood for decomposing fungi and floral abundance for total species richness (Table 1). Richness of all consumer species groups increased with either plant species richness or the indices of host plant availability for fungi or insects indicating a bottom–up effect going from primary producer richness to consumer richness.

Table 1. Model output for GLM negative binomial models using site (n = 130) richness of plants, mosses, lichens, producers (plants, mosses and lichens), symbiotic fungi, decomposing fungi, detritivores (poisson), flying insects, predatory arthropods, herbivores, consumers (fungi and arthropods), all groups, eDNA fungi, eDNA eukaryotes, DNA flying insects. Estimates, p-values (* < 0.05, ** < 0.01, *** < 0.001) and standard errors (in parentheses) are given. Explanatory variables are colored according to ecospace components: position – light grey, expansion – grey, continuity – dark grey, co-variables – white. Hatched: variable not relevant for species group (Supplementary material Appendix 1 Table A3). Litter mass and soil organic C (silver) is part of position for plant, moss, lichen and producer models.

	Dependent variable														
	Plants	Mosses	Lichens	Producers	Symbiotic fungi	Decomposing fungi	Detritivores	Flying insects	Predatory arthropods	Herbivores	Consumers	All groups	eDNA fungi	DNA flying insects	DNA eukaryotes
Intercept	3.580*** (0.058)	2.761*** (0.083)	1.533*** (0.157)	4.002*** (0.065)	2.801*** (0.104)	3.016*** (0.096)	3.103*** (0.033)	3.314*** (0.029)	3.807*** (0.032)	3.665*** (0.035)	5.184*** (0.021)	5.472*** (0.039)	5.633*** (0.026)	4.307*** (0.026)	6.562*** (0.034)
Ecological species pool (log)	0.257*** (0.038)			0.179*** (0.030)											
Soil pH	0.159*** (0.037)			0.143*** (0.032)			0.061** (0.020)		0.032 (0.027)			0.064** (0.021)	−0.136*** (0.033)		
Soil pH^2									−0.040* (0.016)						
Soil fertility	0.119** (0.040)	−0.117* (0.048)	−0.323*** (0.069)	−0.040 (0.033)	−0.024 (0.052)							0.053* (0.022)		0.069* (0.031)	0.084** (0.027)
Soil fertility^2	−0.111*** (0.026)	−0.109** (0.037)		−0.080*** (0.021)	−0.132*** (0.038)							−0.071*** (0.014)			−0.088*** (0.021)
Soil moisture	0.138*** (0.041)	0.257*** (0.042)	0.097 (0.067)	0.120*** (0.025)			−0.056* (0.026)		0.041* (0.018)				−0.104*** (0.028)		0.116*** (0.027)
Soil moisture^2	0.179*** (0.045)		0.221* (0.099)	0.120** (0.037)											
Light intensity					−0.128* (0.060)	−0.138* (0.056)	−0.157*** (0.024)	0.118*** (0.033)	−0.048* (0.021)		−0.081*** (0.016)			0.176*** (0.030)	
Air temperature								0.079* (0.032)	0.077*** (0.019)	0.124*** (0.024)	0.065*** (0.015)				
Boulder (PA)			0.617** (0.234)	0.234* (0.092)											
Litter mass	−0.134** (0.042)														
Litter mass (log)		0.133* (0.062)				0.358*** (0.064)									
Soil organic C	−0.140** (0.046)						0.079** (0.027)	0.100*** (0.029)							
Soil organic C (log)												0.084*** (0.019)			
Plant richness (log)						0.205*** (0.044)	0.093*** (0.021)	0.157*** (0.029)		0.270*** (0.023)			0.204*** (0.032)	0.121*** (0.029)	
Flower abundance (log)												0.076*** (0.018)			
Dung (PA)					0.279** (0.096)	0.343*** (0.096)						0.100** (0.037)			
Dead wood volume						0.090* (0.042)									
Dead wood volume (log)													0.075** (0.028)		
Fungi symbiont plants													0.064* (0.029)		

(Continued)

Table 1. Continued.

	Dependent variable														
	Plants	Mosses	Lichens	Producers	Symbiotic fungi	Decomposing fungi	Detritivores	Flying insects	Predatory arthropods	Herbivores	Consumers	All groups	eDNA fungi	DNA flying insects	DNA eukaryotes
Fungi symbiont plants (log)					0.417*** (0.062)										
Insect host plant availability									0.073*** (0.018)						
Insect host plant availability (log)											0.150*** (0.013)				
Shrub layer		0.268* (0.118)	1.063*** (0.139)	0.343*** (0.060)	0.396** (0.121)	0.616*** (0.117)	0.188*** (0.049)		0.098* (0.044)	0.126* (0.050)	0.252*** (0.032)	0.312*** (0.040)			
Density of large trees (log)							0.107*** (0.020)								
Temporal continuity	0.125*** (0.030)			0.087*** (0.026)											
Natural landscape		0.114* (0.048)							−0.056** (0.019)	−0.056* (0.023)			−0.067* (0.029)		
Soil pH variability (log)					0.133** (0.043)								0.058* (0.027)		
Soil fertility variability (log)								0.058 (0.031)						0.044 (0.028)	
Soil moisture variability (log)							0.041* (0.019)	0.046 (0.029)	0.035* (0.017)					0.065* (0.027)	
Shrub layer variability	0.173*** (0.037)														

The presence of a shrub layer had a consistent and positive effect on the richness of most response groups. We found very few significant effects of within-site heterogeneity on species richness indicating that these were of little importance compared to the effects of between-site variability (Table 1).

In general, we found linear richness responses to underlying abiotic gradients, with the exception of unimodal responses of predatory arthropods to pH, and bimodal responses of lichens, vascular plants and producers to soil moisture. For soil fertility, we observed unimodal responses for vascular plants, mosses, symbiotic fungi as well as the pooled groups of producers and total species richness (Fig. 4).

Models for 'genetic richness' of soil and insect trap DNA were in the lower range of model performance with cross-validated R^2 values of 21% for eukaryotes, 31% for fungi and 24% for flying insects. The correlations between OTU numbers and species richness were significantly positive, but much higher between fungal OTUs and observed fungal richness (Spearman Rho = 0.39, $p < 0.001$) and between flying insect OTUs and observed flying insects (Spearman Rho = 0.51, $p < 0.001$) than between eukaryote OTUs and total observed species richness (Spearman Rho = 0.22, $p = 0.01$). This finding may be explained by the lower variability of the eukaryote marker allowing for discrimination at a higher taxonomic level (genus and family) than the species level for observed species richness. Furthermore, the high number of eukaryote OTUs (Supplementary material Appendix 1 Fig. A2) may point to the soil samples holding a large number of microeukaryotes not found in the inventoried data set. While fungi and flying insects confirmed the consistent positive response to plant richness, none of the DNA groups responded to presence of a shrub layer (Table 1). Soil pH, moisture and fertility affected soil fungal and eukaryotic DNA richness in various ways indicating the importance of the soil environment for its biota (Table 1).

We found no justification for including a random variable (generalized linear mixed model) to account for spatial patterns in the data and only two of 15 models (the flying insects and DNA flying insects models) showed significant spatial autocorrelation after modelling. Spatial signals seem to be of minor importance in this study.

Discussion

Across major terrestrial ecosystems within a region, as much as 77% of the variation in multi-taxon richness was accounted for by our models. The remarkably high explanatory power arose after grouping species into producers (autotrophic organisms) and consumers (heterotrophic organisms). Studies assessing the surrogacy power of multiple environmental variables on multiple taxonomic groups simultaneously, are rare. A meta-study found the surrogacy power of environmental variables to be very poor compared to taxonomic surrogacy (Rodrigues and Brooks 2007) while multi-metric site-conditions explained 48% of variation in total species richness of a range of taxa (ants, beetles, spiders, wasps, flies, butterflies, reptiles, birds,

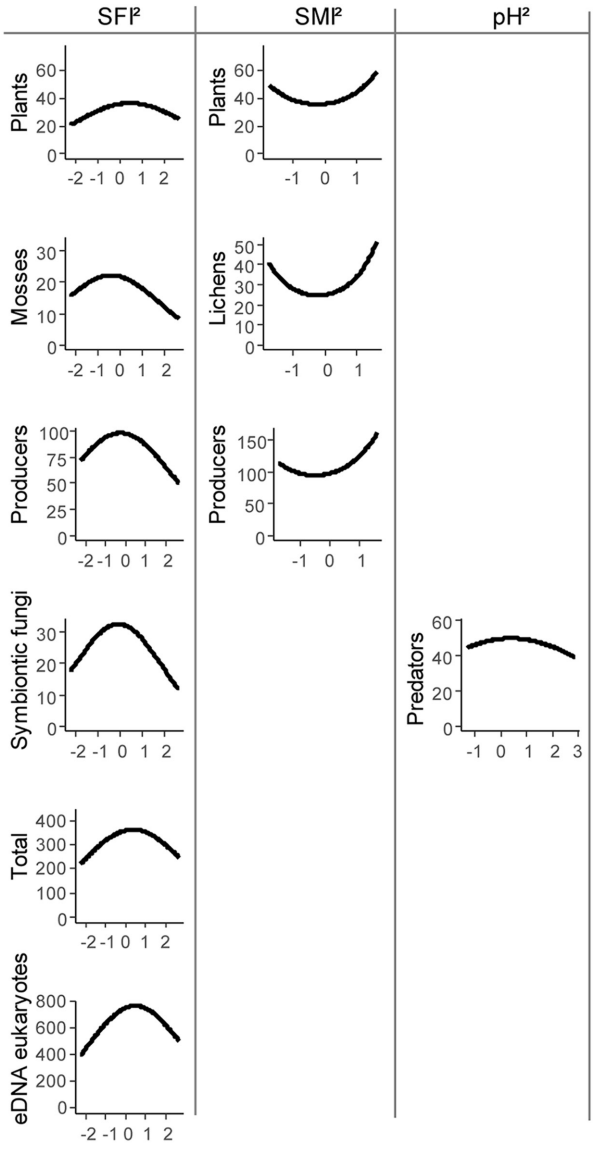

Figure 4. Relationships between significant squared ecospace position terms for soil fertility (SFI), soil moisture (SMI) and pH and the species richness of plants, mosses, lichens, producers, symbiotic fungi, predatory arthropods, total (producers + consumers) and eDNA eukaryotes in the respective multiple regression models.

vascular plants, bryophytes and lichens) in Australian woodlands (Oliver et al. 2014). Our regression models for individual species groups show considerable variation in the selection of variables and this could easily lead to the erroneous conclusion that each taxonomic group needs individual consideration. Nevertheless, the summed predictions derived from models dedicated to taxonomically and ecologically more specialized species groups explained less variation in observed α-diversity than the two models based on high-level aggregation. This level of generalization is striking considering the contrasting life history traits and modes of resource acquisition of the species aggregated as producers or consumers, and it challenges commonly expressed concerns that α-diversity is necessarily contingent on taxonomy and ecology (Gaston 1996, Vessby et al. 2002, Myšák and Horsák 2014).

On the other hand, we found a large drop in explained variation when we tried to aggregate producers and consumers and model all species in one model. This result emphasizes the fundamental difference between sessile autotrophic organisms, whose resource acquisition is largely controlled by abiotic conditions, and heterotrophic organisms, whose resource acquisition relies on biotic resources. The important split between heterotrophic and autotrophic organisms is underpinned by the contrasting role of ecospace position and expansion in the producer and consumer models. Further, plant richness is an important predictor of consumer richness, but to avoid circularity plant richness is excluded from the total richness model.

Based on island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Hanski 1998) we would have expected that ecospaces continuous at larger spatial and temporal extent would increase the probability of immigration and decrease the risk of extinction. Surprisingly, spatiotemporal continuity played a negligible role in explaining multitaxon species richness. Only temporal continuity appeared as a small significant effect in the model of vascular plants and in the producer model. This result does not preclude continuity playing an important role in other biomes or geographical contexts (Nordén et al. 2014). The species pool index for vascular plants emerged with a significant positive effect in the models of vascular plants and producers. This supports the biogeographic theory that species pools founded in evolutionary and historical timescales have lasting impacts on current biodiversity (Zobel 1997). The consistent positive effects of vascular plant richness and host plant indices on fungal and insect richness (Fig. 3b, Table 1) corroborates a similar species pool effect for consumers (Brändle and Brandl 2001). Despite recent advances in the translation of eDNA data into diversity metrics (Frøslev et al. 2017, Zinger et al. 2019), the relatively poor performance of models for DNA groups might point to remaining metagenomic challenges (Bálint et al. 2016, Zinger et al. 2019) or sampling issues (e.g. soil eDNA sampling only covered approximately 0.0025% of the site area). It is also possible however that the variation in below-ground and above-ground biodiversity is determined by different factors and that ecospace expansion in particular may need to be refined to include and differentiate between organic matter pools that support below-ground biodiversity (Baran et al. 2015).

The most consistent predictors of consumer richness were the presence of a shrub layer and high vascular plant richness. Specialized organic matter, such as dead wood and dung were found to be important to fungal and insect richness (Hanski and Cambefort 1991, Stokland et al. 2012), judged from their representation in the detailed species group models.

Our study indicates a bottom–up regulation of species richness, emphasizing the importance in land use and focused nature management of the build-up of vegetation and the differentiation of plant species richness and vegetation structure. The importance of expansion variables to a range of consumer

groups also implies that conservation managers should ensure effective protection against harvesting and homogenizing of organic matter such as live vegetation, flowers and dead wood. Our results support the notion of large herbivores as keystone species promoting local richness by suppression of dominant plants (Bakker et al. 2016), as long as the grazing regime does not obstruct the annual buildup and flowering of the herb layer as well as the long-term buildup of complex vegetation including a shrub layer, veteran trees and dead wood. The provision of large dung and the occasional damage to live trees should be considered instrumental to the diversification of organic matter. We envision that the role of natural dynamic processes for the diversification of organic matter – not least in the soil (Andriuzzi and Wall 2018) – will be a promising field of research in future conservation studies.

To mitigate the biodiversity crisis, there is a need for ecological rules and principles to inform conservation planning and restoration actions (Peters et al. 2016). Without disregarding the scale dependence of biodiversity (Crawley and Harral 2001, Ejrnæs et al. 2018) and the importance of endemism and threatened species (Orme et al. 2005), our study has demonstrated unprecedented potential for generalization of multi-taxon species richness responses to environmental variation, supporting our hypothesis of α-diversity as a predictable property of a low-dimensional ecospace. Acknowledging the explorative nature of our study, future studies are needed to test the causal mechanisms behind the observed correlations and to elucidate how land use and land use changes impacts ecospace variation.

Speculations

We are witnessing a pervasive, global biodiversity crisis where human resource exploitation (provisioning ESS) is the ultimate cause of biodiversity loss. Amidst this crisis, we are concerned that the arguments for biodiversity benefits or risks to humanity have led to exaggeration and loss of focus. We analyzed sites ranging in richness from 119 to 499 species per site and we managed to account for almost 77% of the variation in multi-taxon richness using just a few ecological dimensions (ecospace). The most diverse sites were in areas designated for biodiversity conservation, whereas intensive farmland designed to optimize provisioning ESS was always species poor. Our results confirm a strong tradeoff between provisioning ESS and the extent of natural habitats and biodiversity. Our study had unprecedented taxonomic and environmental coverage. Although we studied one of the most intensively cultivated countries worldwide, we found no indication of synergy between biodiversity and human resource acquisition and no signs of ecosystems collapsing due to loss of diversity. We stress the tradeoff, but acknowledge contexts where diversified crops may benefit productivity, stability and pollination or where low-intensity human exploitation may buffer against habitat destruction from intensified land use. In conclusion, we believe there is a strong need to continue basic research on biodiversity, as well as applied research directly focused on biodiversity conservation and restoration.

Data availability statement

All scripts, ecological data, sequence data and links to data repositories necessary to run the ecological/statistical analyses are available on GitHub <https://github.com/tobiasgf/biowide_synthesis>.

Acknowledgements – We thank Greg Newman for field and laboratory support. Figure 1 is reprinted from: Ejrnæs, R., Frøslev, T. G., Høye, T. T., Kjøller, R., Oddershede, A., Brunbjerg, A. K., Hansen, A. J. and Bruun, H. H. 2018. Uniquity: a general metric for biotic uniqueness of sites. – Biol. Conserv. 225: 98–105. Copyright (2018), with permission from Elsevier.
Funding – RE, IG, TL, US, LD, HHB, TGF, CF and AKB were supported by a grant from VILLUM FONDEN (Biowide, VKR-023343). JCS considers this work a contribution to his VILLUM Investigator project 'Biodiversity Dynamics in a Changing World' funded by VILLUM FONDEN (grant 16549).
Author contributions – A. K. Brunbjerg and R. Ejrnæs contributed equally to this work. RE conceived the research idea and study design. All authors except LD, ATC, TTH and J-CS collected the field data. AKB, RE, LD, TTH and TGF planned and performed the analyses. RE, AKB, HHB and TTH led the writing of the paper. All authors contributed to writing and revising the paper.
Conflicts of interest – The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Andriuzzi, W. S. and Wall, D. H. 2018. Soil biological responses to, and feedbacks on, trophic rewilding. – Phil. Trans. R. Soc. B 373: 20170448.
Bakker, E. S. et al. 2016. Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. – Proc. Natl Acad. Sci. USA 113: 847–855.
Bálint, M. et al. 2016. Millions of reads, thousands of taxa: microbial community structure and associations analyzed via marker genes. – FEMS Microbiol. Rev. 40: 686–700.
Baran, R. et al. 2015. Exometabolite niche partitioning among sympatric soil bacteria. – Nat. Commun. 6: 8289.
Blaxter, M. et al. 2005. Defining operational taxonomic units using DNA barcode data. – Phil. Trans. R. Soc. B 360: 1935–1943.
Brunbjerg, A. K. et al. 2017. Ecospace: a unified framework for understanding variation in terrestrial biodiversity. – Basic Appl. Ecol. 18: 86–94.
Brunbjerg, A. K. et al. 2018. Vascular plant species richness and bioindication predict multi-taxon species richness. – Methods Ecol. Evol. 9: 2372–2382.
Brunbjerg, A. K. et al. 2019. A systematic survey of regional multitaxon biodiversity: evaluating strategies and coverage. – BMC Ecol. 19: 43.
Bruun, H. H. et al. 2020. Simple attributes predict the importance of plants as hosts to the richness of fungi and arthropods. – bioRxiv: 2020.2004.2017.046292.
Brändle, M. and Brandl, R. 2001. Species richness of insects and mites on trees: expanding Southwood. – J. Anim. Ecol. 70: 491–504.
Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information–theoretic approach. – Springer.

Callahan, B. J. et al. 2016. DADA2: high-resolution sample inference from Illumina amplicon data. – Nat. Methods 13: 581–583.
Callahan, B. J. et al. 2017. Exact sequence variants should replace operational taxonomic units in marker-gene data analysis. – ISME J. 11: 2639–2643.
Castagneyrol, B. and Jactel, H. 2012. Unraveling plant–animal diversity relationships: a meta-regression analysis. – Ecology 93: 2115–2124.
Crawley, M. J. and Harral, J. E. 2001. Scale dependence in plant biodiversity. – Science 291: 864.
Danish Ministry of Environment 2015. Danmarks Højdemodel, DHM/Punktsky. Data ver. 2.0, Copenhagen, Denmark, 1-11.
Díaz, S. et al. 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. – Science 366: eaax3100.
Duan, M. et al. 2016. Disentangling effects of abiotic factors and biotic interactions on cross-taxon congruence in species turnover patterns of plants, moths and beetles. – Sci. Rep. 6: 23511.
Dufrêne, M. and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. – Ecol. Monogr. 67: 345–366.
Ejrnæs, R. et al. 2014. Biodiversitetskort for Danmark. Udviklet i samarbejde mellem Center for Makroøkologi, Evolution og Klima på Københavns Universitet og Institut for Bioscience ved Aarhus Universitet. Aarhus Universitet, DCE – Nationalt Center for Miljø og Energi, 96 s. – Videnskabelig rapport fra DCE – Nationalt Center for Miljø og Energi nr. 112.
Ejrnæs, R. et al. 2018. Uniquity: a general metric for biotic uniqueness of sites. – Biol. Conserv. 225: 98–105.
Ellenberg, H. et al. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. – Verlag E. Goltze KG.
Ellis, C. J. 2012. Lichen epiphyte diversity: a species, community and trait-based review. – Perspect. Plant Ecol. Evol. Syst. 14: 131–152.
Elton, C. S. 1966. The pattern of animal communities. – Chapman & Hall.
Fagerström, T. and Westoby, M. 1997. Population dynamics in sessile organisms: some general results from three seemingly different theory-lineages. – Oikos 80: 588–594.
Fløjgaard, C. et al. 2019. Predicting provenance of forensic soil samples: linking soil to ecological habitats by metabarcoding and supervised classification. – PLoS One 14: e0202844.
Frøslev, T. G. et al. 2017. Algorithm for post-clustering curation of DNA amplicon data yields reliable biodiversity estimates. – Nat. Commun. 8: 1188.
Frøslev, T. G. et al. 2019. Man against machine: do fungal fruitbodies and eDNA give similar biodiversity assessments across broad environmental gradients? – Biol. Conserv. 233: 201–212.
Futuyma, D. J. and Agrawal, A. A. 2009. Macroevolution and the biological diversity of plants and herbivores. – Proc. Natl Acad. Sci. USA 106: 18054.
Gaston, K. J. 1996. Biodiversity – congruence. – Prog. Phys. Geogr. 20: 105–112.
Hanski, I. 1998. Metapopulation dynamics. – Nature 396: 41–49.
Hanski, I. and Cambefort, Y. 1991. Dung beetle ecology. – Princeton Univ. Press.
Hartig, F. 2016. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. – R package ver. 0.1.0. CRAN/GitHub.
Hartvig, P. (ed.) 2015. Atlas Flora Danica. – Gyldendal.
Hilbe, J. M. 2011. Negative binomial regression. – Cambridge Univ. Press.
Jepson, P. et al. 2018. Governing with nature: a European perspective on putting rewilding principles into practice. – Phil. Trans. R. Soc. B 373: 20170434.
Johnson, J. B. and Omland, K. S. 2004. Model selection in ecology and evolution. – Trends Ecol. Evol. 19: 101–108.
Lawton, J. H. 1999. Are there general laws in ecology? – Oikos 84: 177–192.
MacArthur, R. and Wilson, E. 1967. The theory of island biogeography. – Princeton Univ. Press.
Moeslund, J. E. et al. 2019. Light detection and ranging explains diversity of plants, fungi, lichens and bryophytes across multiple habitats and large geographic extent. – Ecol. Appl. 29: e01907.
Myšák, J. and Horsák, M. 2014. Biodiversity surrogate effectiveness in two habitat types of contrasting gradient complexity. – Biodivers. Conserv. 23: 1133–1156.
Nordén, B. et al. 2014. Effects of ecological continuity on species richness and composition in forests and woodlands: a review. – Ecoscience 21: 34–45.
Oliver, I. et al. 2014. What do site condition multi-metrics tell us about species biodiversity? – Ecol. Indic. 38: 262–271.
Orme, C. D. L. et al. 2005. Global hotspots of species richness are not congruent with endemism or threat. – Nature 436: 1016–1019.
Peters, M. K. et al. 2016. Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. – Nat. Commun. 7: 13736.
Prober, S. M. et al. 2015. Plant diversity predicts beta but not alpha diversity of soil microbes across grasslands worldwide. – Ecol. Lett. 18: 85–95.
Rodrigues, A. S. L. and Brooks, T. M. 2007. Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. – Annu. Rev. Ecol. Evol. Syst. 38: 713–737.
Stokland, J. N. et al. 2012. Biodiversity in dead wood. – Cambridge Univ. Press.
Thomas Chris, D. 2000. Dispersal and extinction in fragmented landscapes. – Proc. R. Soc. B 267: 139–145.
Titeux, N. et al. 2016. Biodiversity scenarios neglect future land-use changes. – Global Change Biol. 22: 2505–2515.
Vessby, K. et al. 2002. Species–richness correlations of six different taxa in Swedish seminatural grasslands. – Conserv. Biol. 16: 430–439.
Westgate, M. J. et al. 2014. Global meta-analysis reveals low consistency of biodiversity congruence relationships. – Nat. Commun. 5: 3899.
White, N. et al. 2008. A comparison of plotless density estimators using Monte Carlo simulation on totally enumerated field data sets. – BMC Ecol. 8: 6.
Zeale, M. R. K. et al. 2011. Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. – Mol. Ecol. Resour. 11: 236–244.
Zinger, L. et al. 2019. DNA metabarcoding – need for robust experimental designs to draw sound ecological conclusions. – Mol. Ecol. 28: 1857–1862.
Zobel, M. 1997. The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? – Trends Ecol. Evol. 12: 266–269.
Zuur, A. F. et al. 2010. A protocol for data exploration to avoid common statistical problems. – Methods Ecol. Evol. 1: 3–14.

Supplementary material (available online as Appendix oik-07145 at <www.oikosjournal.org/appendix/oik-07145>). Appendix 1.